Anthracothere dental anatomy reveals a late Miocene Chado-Libyan bioprovince

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Recent discovery of an abundant and diverse late Miocene fauna at Toros-Ménalla (Chad, central Africa) by the Mission Paléoanthropologique Franco-Tchadienne provides a unique opportunity to examine African faunal and hominid evolution relative to the early phases of the Saharan arid belt. This study presents evidence from an African Miocene anthracotheriid *Libycosaurus*, particularly well documented at Toros-Ménalla. Its remains reveal a large semiaquatic mammal that evolved an autapomorphic upper fifth premolar (extremely rare in Cenozoic mammals). The extra tooth appeared ≈12 million years ago, probably in a small northern African population isolated by climate-driven fragmentation and alteration of the environments inhabited by these anthracotheriids [Flower, B. P. & Kennett, J. P. (1994) *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 108, 537–555 and Zachos, J., Pagani, M., Sloan, L., Thomas, E. & Billups, K. (2001) *Science* 292, 686–693]. The semiaquatic niche of *Libycosaurus*, combined with the distribution and relationships of its late Miocene species, indicates that by the end of the Miocene, wet environments connected the Lake Chad Basin to the Libyan Sirt Basin, across what is now the Sahara desert.

Anthracotheriidae | Chad | Libya | paleobiogeography | early hominids

Fig. 1. Geographical situation of the Toros-Ménalla fossiliferous area (TM), Djourab Erg, North Chad.

During the late Neogene, global climatic changes resulted in the development of arid environments across vast portions of Africa (1, 2). These modifications in the African environmental setting are thought to have strongly influenced faunal distribution and evolution by reshuffling ecological barriers. In particular, the late Miocene emergence and development of the Saharan arid belt would have had a dramatic impact, as recently illustrated for some Miocene Afrotherian mammals by Douady *et al.* (3). In this context, the central African fauna from Toros-Ménalla (TM), western Djourab erg, northern Chad, discovered in 1997 by the Mission Paléoanthropologique Franco-Tchadienne (refs. 4–6; Fig. 1) represents a crucial data set. This fauna constitutes a unique late Miocene fossil record in northern central Africa.

One of the most interesting features of the TM late Miocene fauna is the abundance of anthracotheriids. The fossil cetartiodactyl family Anthracotheriidae probably originated from the extinct Helohyidae (7) in southeastern Asia during the middle Eocene, with a first record ≈41 million years ago in Myanmar (8). From this area, these mammals spread and diversified in both New and Old Worlds, until the last anthracotheres finally went extinct 2.5 million years ago in Asia (9). During the late Eocene, the family entered Africa for the first time (10). There, Miocene anthracotheriids probably gave rise to the Hippopotamidae (11). The last African anthracotheres were represented by one endemic genus, *Libycosaurus*. The genus penetrated eastern Africa only in Uganda ≈10 million years ago (12), but it is represented by three species from 12 million years ago to

terminal Miocene in northern and central Africa in Tunisia, Algeria, Libya, and in Chad at Toros-Ménalla (6, 13–19).

As for other advanced anthracotheres, morphological and taphonomic evidence indicate that *Libycosaurus* had an amphibious lifestyle (20–22). It consequently can be inferred that the dependence of these mammals on permanent water bodies constrained their ability to disperse. Their temporal and spatial distribution therefore should follow the development of hydrographic pathways linking different African basins.

The particularly abundant and well preserved material referred to *Libycosaurus* at Toros-Ménalla affords evidence on the debated nature of its highly derived dental formula (16, 18) and allows the reconstruction of its evolutionary history in central and northern Africa. These data can be used to examine the paleohydrographic dynamics of northern central Africa in an effort to test the late Miocene Saharan arid barrier model (1, 2). They indicate the existence of a Chado-Libyan biogeographical province exclusive of eastern Africa at the time of the earliest known hominids.

Results and Discussion

The parsimony analysis performed on anatomical characters of the most representative species of advanced selenodont anthra-
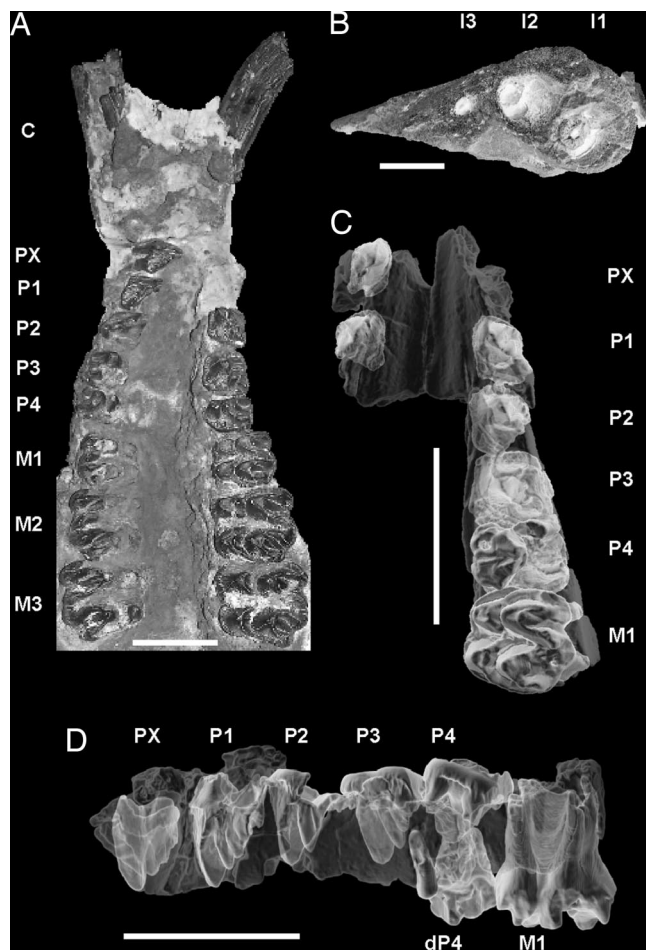

Fig. 2. Evidence for presence of a fifth premolar in *Libycosaurus*. (*A*) Maxillary of *Libycosaurus* from Toros-Ménalla, Chad (TM276-01-08) in occlusal view, displaying the ever-growing canine (C), the premolar row (P^X–P^4) and the molar row (M^1–M^3). (Scale bar: 5 cm.) (*B*) Premaxilla (TM273-01-03) in occlusal view showing the three incisor alveoli. (*C* and *D*) Microtomography of juvenile maxillae of *L. petrocchii* from Toros-Ménalla, Chad (TM233-01-01) in occlusal (note dP^1, dP^2, and dP^3 alveoli) (*C*) and lateral (*D*) views showing the permanent teeth inside the bone (transparent). All five definitive premolars were ready to erupt.

cotheres indicates that *Libycosaurus* was a monophyletic genus. Its evolutionary history was exclusively African, and its sister group was the Asian *Merycopotamus* (see Fig. 3; see *Supporting Text*, which is published as supporting information on the PNAS web site, for analysis details). It is important to note that semiaquatic habits also are proposed for *Merycopotamus* (21, 23), implying that this ecology was a plesiomorphic condition in *Libycosaurus*. The monophyly of *Libycosaurus* is independently supported by the peculiar features of its dentition discussed below.

The Innovative Dentition of *Libycosaurus*. Our studies of well preserved dentitions of *Libycosaurus* demonstrate the surprisingly regular occurrence of a "supernumerary" fifth upper premolar on all known maxillae (Fig. 2 *A*, *C*, and *D*). This tooth is absent in all other known anthracotheriid genera (see *Supporting Text*). Microtomographic synchrotron x-ray investigation performed on a juvenile specimen (TM233-01-01) with a deciduous dentition partially replaced by permanent teeth (Fig. 2 *C* and *D*) confirms our anatomical observations. On this specimen, only one highly worn deciduous premolar remains functional and

is set just mesially to the first permanent molar. The other deciduous premolars already are shed, but their alveoli still are visible. The entire set of permanent premolars is embedded in the maxilla, close to eruption. The permanent premolar below the remnant worn deciduous premolar displays the bicuspidate morphology typical of fourth upper permanent premolars (P^4) in Anthracotheriidae (Fig. 2 *C* and *D*). The presumed P^3 bears two accessory cusps on its distolabial crest, a condition congruent with that observed in advanced bothriodontines. In *Libycosaurus*, the accessory cusp number on that crest increases from P^3 to the P^1. This morphological gradient is extended to the extra premolar crown, which accordingly displays five accessory cusps. This tooth therefore seems to follow the same developmental pathway as the other premolars because it develops a morphology expected for the most mesial premolar.

Furthermore, the extra premolar crown in *Libycosaurus* cannot be interpreted as a premolariform canine because it is positioned just distal to a large ever-growing tooth embedded in the maxilla (Fig. 2*A*). The latter is a canine and not a caniniform incisor (contra 18). This conclusion is further supported by the presence of three incisiform permanent teeth set on the premaxilla, as initially described for Libyan material (17) and as observed on the new Chadian material (Fig. 2*B*). The I^1 and I^2 both display prolonged-growing roots and are accompanied by a reduced I^3. Because of inconsistencies in recognizing homologous teeth among placental mammals (e.g., ref. 24), we have identified the new *Libycosaurus* fifth premolar as P^X. The P^X cannot be a retained dP^1 (or any other dP). Its morphology matches that of permanent premolars, differing only by its smaller size and the reduction of its distal basin. Moreover, as demonstrated on the scanner reconstruction, the eruption of P^X was just before P^1. Finally, dP^1, dP^2, and dP^3 alveoli coexist with the P^X in specimen TM233-01-01. It is still unclear whether P^X replaced a dP^X. The mandible displays only four premolars and the usual P^X distal wear implies its occlusion with the P_1.

The P^X described above is unambiguously present in the Chadian and Libyan *Libycosaurus petrocchii*. For the Tunisian *Libycosaurus anisae*, we follow Pickford (18), who affirmed to have seen the same dental formula as in the Libyan *L. petrocchii*. The presence of the P^X in the specimens from Uganda and Algeria cannot be assessed because of their fragmentary condition. This uniquely derived dental feature therefore is reported in two species of *Libycosaurus* from three distinct regions: from the Gabes Basin between 9 and 12 million years ago (13, 14) and from the Lake Chad Basin and the Sirt Basin during the terminal Miocene (6, 17, 20).

Placental mammals usually develop two sequent dentitions: an initial deciduous dentition in juveniles, later replaced by a permanent dentition. Long before the beginning of the Cenozoic, the latter dentition stabilized at 44 teeth (3 incisors, 1 canine, 4 premolars, and 3 molars, noted 3-1-4-3), constituting the primitive dental formula for all subsequent placental mammals. During the Cenozoic, most placental lineages experienced increasing dietary and other specializations resulting in morphofunctional losses of teeth, therefore, in derived smaller dental formulae (25). In contrast, dental formula increases are most frequently teratologies. Consequent supernumerary teeth generally produce malocclusion and/or other pathologies (26). Normally shaped bilateral supernumerary teeth are sometimes found in a small number of individuals within a population (for example, numbers cited in ref. 27 indicate an occurrence rate of <8%), but the P^X of *Libycosaurus* cannot be identified as such a supernumerary tooth because it occurs regularly and bilaterally, with a consistent shape, in all 16 observable examined specimens. This mammal therefore exhibits at a generic level the following standard dental formula: 3-1-5-3.

The presence of a standard fifth premolar is seen in the earliest known placental mammal, *Prokennalestes*, from the early Cre-
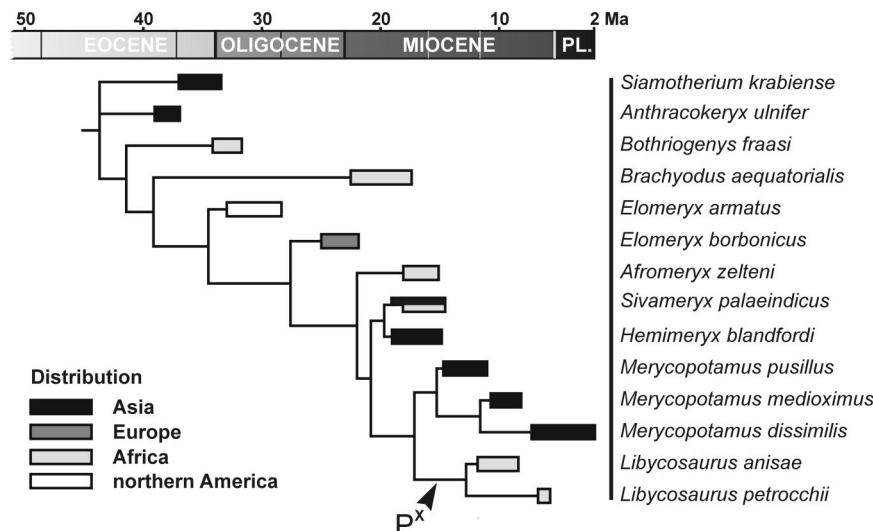
Fig. 3. Most parsimonious tree obtained after parsimony analysis of 14 taxa and 37 cranial and dental characters, illustrating the hypothesis for phylogenetical relationships between the advanced selenodont anthracotheres (67 steps, consistency index = 0.76, retention index = 0.85). The appearance of P^X is indicated by an arrow.

taceous (110 million year ago) of Mongolia (28) and in other early Placentalia. However, for Novacek (24), this condition represents an ancestral condition that was permanently lost before the late Cretaceous. Anthracotheriids originate during the Paleogene and do not show such features outside of *Libycosaurus*. In the latter, this condition therefore is apomorphic. Such a derived increase of a dental formula beyond the primitive 3-1-4-3 was reported in early sirenians (29) and is also known in modern and fossil odontocetes (30). However, these documented cases are definitely rare in the mammalian fossil record (29, 31). Indeed, the P^X of *Libycosaurus*, being a new case of consistent occurrence of a fifth premolar in a placental permanent dentition, appears to be unique among Cenozoic hoofed mammals.

Recent research on the genetics of dental development suggests that such a change of dental formula could result from relatively minor changes in developmental pathways (32, 33). The very low frequency of corresponding phenotypes (29, 31) strongly suggests that the emergence of P^X in *Libycosaurus* was a single event that originally occurred in a single population. This population must have been isolated and of limited size to fix the new feature and, thus, to transmit it to all its descendants, i.e., at least three different species widely distributed across northern and central Africa. Such a scenario fits the theoretical "founder effect" of a pioneer population (34). It also implies that at least some parts of the larger gene pool from which *Libycosaurus* directly emerged were divided into small isolated populations.

Given the specialized semiaquatic habits of this anthracotheriid and its closest relatives, isolation of small populations might have been related to the dislocation, and perhaps the degradation, of the aquatic and wet habitats necessary to sustain those mammals. The area and date to which these unfavorable conditions can be tracked is indicated by the earliest record of the P^X (and of *Libycosaurus*), i.e., in the Gabes Basin, Tunisia, between 10 and 12 million years ago. This original dental feature provides support to the hypothesis, congruent with previous paleoclimatological reconstruction (1, 2), that the Sahara transformed into an arid area at this time (3, 35). We suggest that additional tests of that hypothesis be conducted by seeking evidence of increased endemism of water-dependant vertebrates during the late middle/early late Miocene in the northern half of Africa.

Interpretation of Species Relationships and Distribution in *Libycosaurus*. Our phylogenetic analysis (see *Supporting Text*) provides insights on faunal exchange between Africa and Asia. The close relationships between *Libycosaurus* and the Asian *Merycopotamus* from the Siwaliks of Pakistan implies that the precursors of *Libycosaurus* are to be found within the Asian stock of Bothriodontinae (comprising *Hemimeryx*, *Sivameryx*, and *Merycopotamus*; Fig. 3). Given these relationships and the strictly African occurrence of the P^X strongly supporting the monophyly of *Libycosaurus*, this genus most probably emerged in Africa from an Asian migrant population. Two preceding dispersals of anthracotheriids in Africa were recorded in the late Eocene (36) and in the early Miocene (at 18 million years ago; refs. 20 and 37), respectively. Our phylogenetic reconstruction therefore forecasts a third dispersion event between the first appearance of *Merycopotamus* (20, 23) ≈15 million years ago and the appearance of the first and most archaic species of *Libycosaurus*, *L. anisae* (Fig. 3), known from 9 to 12 million years ago. This event suggests wet enough conditions for the spread of water-dependent anthracotheriids within Africa during this interval.

The emergence of the P^X in a small isolated population ≈12 million years ago may suggest a geographic fragmentation of the wet habitat of *Libycosaurus*. Roughly contemporaneous to *L. anisae* and equally archaic, *L. algeriensis* also was present between 10 and 12 million years ago in the same northern African basin, the Gabès. This co-occurrence indicates an early speciation event, also possibly correlated with habitat fragmentation. The simultaneous presence of *L. anisae* in Tunisia and Uganda ≈10 million years ago suggests that habitats suitable to semiaquatic mammals occurred continuously from northern Africa to the Western Rift. This continuity was probably soon disrupted, as indicated by the subsequent disappearance of anthracotheriids from eastern Africa. From that time forward, these mammals were confined to northern central Africa until they vanished from the continent after 6 to 7 million years ago.

Given the more derived evolutionary status of *L. petrocchii* compared with *L. anisae* (Fig. 3; see *Supporting Text*), it is probable that the latter (or a close relative) constituted the stock from which the more advanced *Libycosaurus* species derived. This younger species is present both in Chad and Libya. Wherever the speciation event occurred, the distribution of this semiaquatic species strongly supports a hydrographic connection
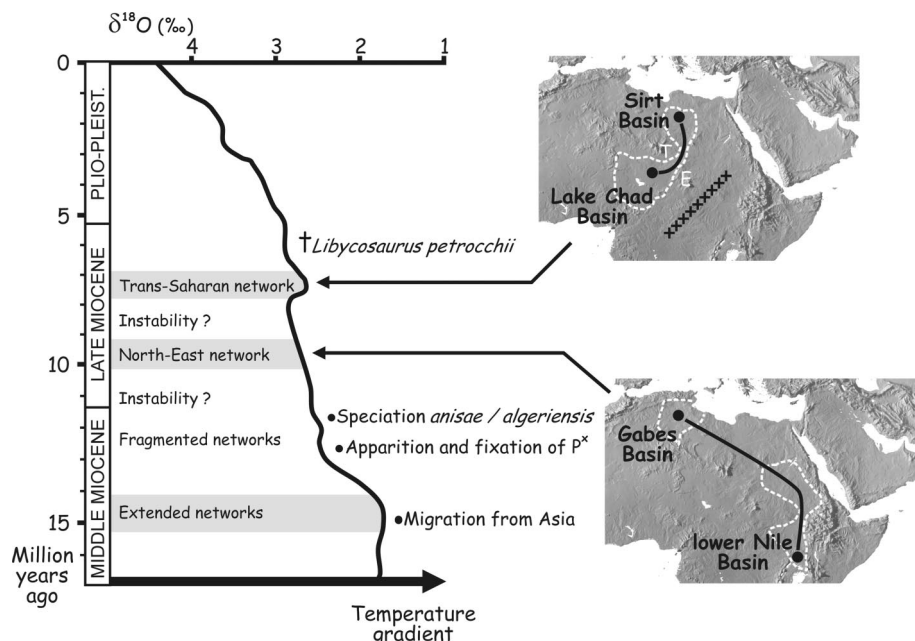
Fig. 4. Evolution and dispersal events of the genus *Libycosaurus* compared with the climate proxy data (evolution of δ ^{18}O after ref. 5) during the middle-late Miocene. Interpretations concern environmental changes in the Saharan area, notably hydrographical networks. On upper northern Africa map, T is Tibesti and E is Ennedi.

younger than 9 million years ago between the Lake Chad Basin and the Libyan Sirt Basin, in a relation excluding eastern Africa (Fig. 4). Today, those basins are separated by almost 2,000 km of arid to hyperarid lands, principally the Djourab and the Libyan deserts. During the late Miocene, paleo-Lake Chad formed an occasionally hyperdeveloped fluviolacustrine complex extending north to the 18th or 19th parallel (6). The Sirt Basin also was possibly drained by a large Eosahabi river that originated on the slopes of the Tibesti Mountains (38). The low elevated area that currently separates the Tibesti and the eastern Ennedi therefore could be considered as the possible route for the dispersions of *Libycosaurus* species (Fig. 1).

Evolution of the Sahara and Its Fauna During the Late Miocene. The evolution of *Libycosaurus* suggests a complex environmental history for the Sahara region. Our model or "paleoscenario," based on paleontological and geological observations, is consistent with paleoclimatic records (Fig. 4; refs. 1 and 2). Other mammals provide congruent evidence with the main phases of Saharan evolution as described above. Vicariant speciations in Macroscelidea occurred ≈12 million years ago in relation to initial aridification (3). The possibly semiaquatic *Kenyapotamus* is reported from both Tunisia and Kenya ≈9 to 10 million years ago (39) and indicates an early late Miocene hydrographic connection between eastern and northern Africa. The occurrence of distinct hippopotamid lineages in Chad at TM and in Kenya at Lothagam (40, 41) further attests to a hydrographic discontinuity between eastern and central Africa during the final Miocene. For this later phase, *Libycosaurus* and hippopotamids help to delineate a Chado-Libyan faunal province isolated from an eastern African faunal province, at least for water-dependent taxa. Some terrestrial mammals also support such a bioprovince. The Chadian *Machairodus kabir* (Felidae) and the closely related material from Sahabi represent a lineage not found contemporaneously in eastern Africa (42).

Distribution through time and space of water-dependent taxa therefore appears to hold valuable information on paleogeography (in terms of hydrographic connections between basins) and on past environments (in terms of dry/wet condition alternations). These data are critical for accurately assessing the environmental framework of African faunal evolution. For the earliest steps of the evolution of the genus *Libycosaurus*, more fossils are needed to confirm the model of Saharan biogeography proposed here. More middle to early late Miocene data from the south Mediterranean margin to the meridional Sahara region would allow a more detailed model with a wider scope and bear upon faunal exchanges between Africa and Eurasia during this period.

The late Miocene Chado-Libyan faunal province described here also bears on overall faunal dynamics in continental Africa. Other mammals may have been less constrained in their ability to disperse than semiaquatic species, but nevertheless, would have been water-dependent. Among others, this dependence is found in most primates and, notably, great apes and early hominids. At TM, *Libycosaurus* was recovered in the same localities as the earliest known hominid *Sahelanthropus tchadensis* (4–6). As a consequence, the likely continuous wet habitats from the southern Lake Chad basin to the Libyan Mediterranean margin might have constituted a possible means for trans-Saharan dispersal. This lack of arid barrier, therefore, dramatically widens the African window in which late Miocene hominids are expected to have occurred and might yet be recovered.

Materials and Methods

Taxa and Phylogenetic Relationships. *Libycosaurus* species are characterized by a marked orbital elevation above the cranial roof, a marked elevation of the nasal aperture implied by the long frontal symphysis between the premaxillae, a long auditory tube, and a very dense tympanic bulla. All those features tend to be present in vertebrates living at the air/water interface (20, 43). It is therefore possible to infer a behavior similar to that of hippopotamids for this genus, in agreement with refs. 21, 22, 36, and 37.

Three *Libycosaurus* species have been described: *L. anisae* from Bled Douarah in southern Tunisia (10–12 million years ago; ref. 13), Djebel Krechem in northern Tunisia (≈9 million years ago; refs. 14 and 20), and the Kakara Formation in Uganda (≈10 million years ago; ref. 12). *L. algeriensis* is known from Bir

el Ater 2 in Algeria (10–12 million years ago; ref. 15) and *L. petrocchii* is from the terminal Miocene locality of Sahabi in Libya (16–17).

Systematic studies of >230 cranial and postcranial specimens from the deposits of Toros-Ménalla (Anthracotheriid Unit) place these Chadian anthracotheres in the genus *Libycosaurus* (20) based on upper molar tetracuspidy with undivided mesostyle, palatine groove with the main palatine foramina in anterior position, numerous accessory cusps on premolars, mandibular notch not marked, and reduced number of lower incisors. The species *L. petrocchii* was recognized at TM (6, 20) by its measurements (larger than *L. anisae*), the absence of a loop-like hypoconulid on M_3, and its monoradiculate P^4. The same species is known from Sahabi, Libya.

We examined the biogeographical history of *Libycosaurus* based on the phylogenetic relationships among its species and close relatives. Relationships were inferred through cladistic analysis performed on 14 advanced selenodont anthracotheriids and employing 37 craniomandibular and dental characters (see *Supporting Text*). Most parsimonious trees were generated by using the branch-and-bound algorithm of PAUP 4.0 *β*10 (44).

Dental Formula Analysis. Previous descriptions of the upper dental formula of *Libycosaurus* postulated either the presence of a premolarifom-reduced canine or an upper premolar count exceeding $n = 4$ (16, 18). It must be noted that all anthracotheriids purportedly closely related to *Libycosaurus*, notably *Merycopotamus*, exhibit a fully developed caniniform upper canine (18, 23), whereas all other Anthracotheriidae and almost all Neogene placental mammals retain at most four premolars.

The study of the upper dental formula in *Libycosaurus* was performed on specimens from the late Miocene of central and northern Africa, excluding the meager fossils of *L. algeriensis* and *L. anisae* (Uganda). The studied sample comprised original specimens from Toros-Ménalla, Chad, housed in the Centre National d'Appui à la Recherche, N'Djamena, Chad, including 13 pertinent specimens listed in *Supporting Text*. Two complete premaxillae with

I1–I3 alveoli (TM97-02-06 and TM273-01-03; Fig. 2*B*) allowed us to establish the upper dental formula of the Chadian anthracotheriid. Data on the material from Bled Douarah (Tunisia) was included from discussions and figures in refs. 13 and 18.

Within the observed sample, direct examination of all palates exhibiting the complete upper dentition or the corresponding tooth alveoli allowed the determination of the correct dental formula (Fig. 2). The analysis included tomographic scanning of unerupted teeth performed at the European Synchrotron Research Facilities with a monochromatic x-ray beam and a linear germanium detector (pixel size 350 microns). Absorption contrast between bones and teeth is very low on the Chadian sample because of diagenesis, hence monochromaticity was important to avoid the beam hardening effect obtained with medical scanners by using conventional x-rays.

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EVOLUTION